

Genome-wide analyses have identified more than 100 MADS-box genes in *Arabidopsis*, classified into type I and type II lineages, indicating significant evolutionary diversification and functional specialization. Expression profiling studies further demonstrate coordinated yet distinct patterns during key developmental stages such as embryogenesis, seed maturation, and fruit development (Alvarez-Buylla et al., 2000; Parenicová et al., 2003).

A characteristic feature of MADS-box proteins is their ability to form dimers and higher-order complexes, which enhance regulatory specificity. These interactions underpin the “quartet model,” where multimeric protein complexes bind to multiple cis-elements to regulate floral organ identity (Egea-Cortines et al., 1999; Theissen and Saedler, 2001). Such combinatorial control mechanisms significantly expand the functional diversity of the MADS-box family (Honma and Goto, 2001; Jack, 2001). The molecular framework underlying these interactions is illustrated in Figure 1.

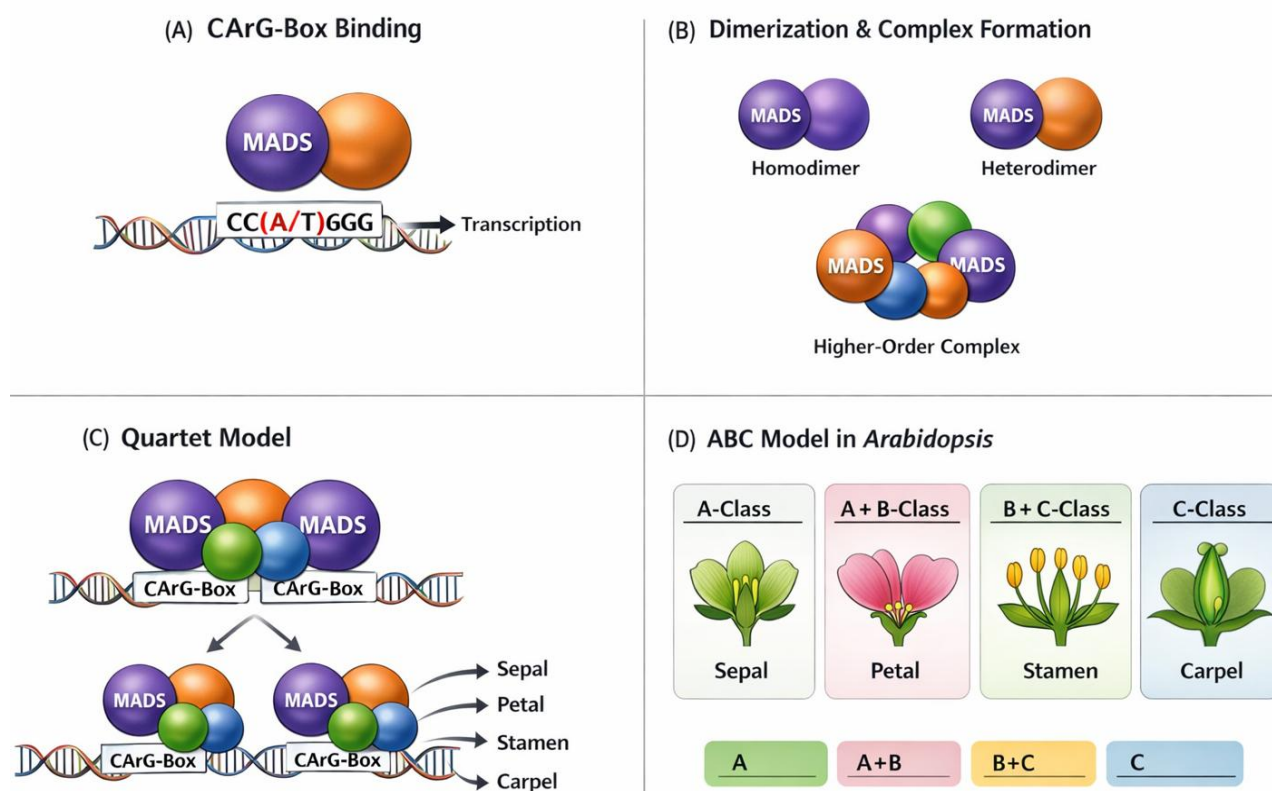


Figure 1 Regulatory framework of MADS-box transcription factors in plant development

Note: (A) MADS-box transcription factors bind to conserved CArG-box cis-regulatory elements [CC(A/T)₆GG] located in the promoter regions of target genes, initiating transcriptional regulation of downstream developmental processes. (B) MADS-box proteins undergo homo- and heterodimerization and can assemble into higher-order multimeric complexes, which enhance DNA-binding specificity and enable combinatorial control of gene expression. (C) Quartet model of floral organ specification, illustrating tetrameric complexes of MADS-box proteins binding to two adjacent CArG-box elements to regulate target genes involved in the determination of floral organ identity, including sepals, petals, stamens, and carpels. (D) ABC model of floral organ identity in *Arabidopsis thaliana*, showing that A-class genes specify sepals, A- and B-class genes specify petals, B- and C-class genes specify stamens, and C-class genes specify carpels

Functional studies have demonstrated that specific MADS-box genes, such as B-sister genes and AGAMOUS, play crucial roles in ovule, seed, and floral organ development through transcriptional regulation and feedback loops (Ito et al., 2004; Gómez-Mena et al., 2005). Additionally, advances in techniques such as chromatin immunoprecipitation and transcriptomic analyses have enabled the identification of direct target genes and regulatory networks (Wang et al., 2002; Taverner et al., 2004). Recent studies have further expanded our understanding of MADS-box transcription factors, highlighting their roles in complex gene regulatory networks and evolutionary diversification (Smaczniak et al., 2012; Chen et al., 2018).